On the Reef Corals of the World's Most Northern Atoll (Kure: Hawaiian Archipelago)[1]

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KURE (28°25'N, 178°20'W) forms the northwestern terminus of the Hawaiian Archipelago and constitutes the world's northernmost atoll (Bryan, 1953). The marine geology of the atoll has recently been discussed by Gross et al. (1969). Brief descriptions by visiting scientists and survivors of shipwrecks have presented general aspects of the flora and fauna, principally terrestrial, and the Pacific Ocean Biological Survey Program of the Smithsonian Institution (POBSP) has made some 5 years of observations on the atoll's avifauna (unpublished). Gross et al. (1969) give a short discussion of marine organisms and environmental factors of Kure, Midway, and Pearl and Hermes Reef. Yet detailed descriptions, especially of an ecological nature, are almost totally lacking for all aspects of the marine fauna of Kure. A brief visit to the atoll in the late summer of 1968 on the STYX Expedition of Scripps Institution of Oceanography and 3½ months spent on the atoll with the POBSP (winter and spring, 1969) form the basis for the following observations on the distribution and relative abundance of hermatypic scleractinian corals present there.

GEOLOGICAL HISTORY

Deep drilling on Midway Atoll (28°13'N, 177°23'W), some 80 km east-southeast of Kure, has established the age of the contact with basalt as approximately 15×10^6 years before present (Miocene) (Ladd et al., 1967). The shallow drill hole reached basalt at 155 m, a depth comparable to the top of the Miocene reported from Eniwetok, Bikini, and Kita-Daito-Jima (Ladd et al., 1967). Presently there is no reason to assume that Kure has not had a parallel post-Miocene history.

At least one major interruption in the construction of Kure has occurred as indicated by a marked break in slope at a depth between 73 and 109 m (Fig. 1). That this was the result of a lower stand of sea level is suggested by the fact that Midway shows the same break in slope and that there are several seamounts or banks in the vicinity that appear to form comparable platforms (Fig. 2). This depth range brackets the maximum depth of lagoons reported elsewhere in the Indo-Pacific by Wiens (1962) and the top of the lower zone of recrystallization in the Eniwetok and Bikini drillings reported by Schlanger (1963). A second interruption is indicated by a calcite-aragonite unconformity at approximately 60 m noted in the Midway drillings (Ladd et al., 1967). This interruption may also correlate with the lower limit of the shallowest recrystallized zone reported from Eniwetok and Bikini by Schlanger (1963), and with a seaward terrace and the general depth of lagoons found in the Marshall and Caroline islands by Curray and Newman (personal communication). Presumably the development of Kure was also interrupted at this depth. Curiously, the 17 to 18 m seaward terrace reported by Wiens (1962) as occurring elsewhere in the Pacific is lacking on Kure. The maximum depth of the lagoon (15 m), although certainly reduced by recent sediments and growth, may correspond with this terrace.

CONTEMPORARY REEFS

Shallow Reefs

The shallow-water reefs have arbitrarily been divided into 4 major zones: seaward reef, surface reef (somewhat comparable to a reef flat), back reef, and lagoon reefs. Kure is located in the northeast trade wind belt, giving each reef

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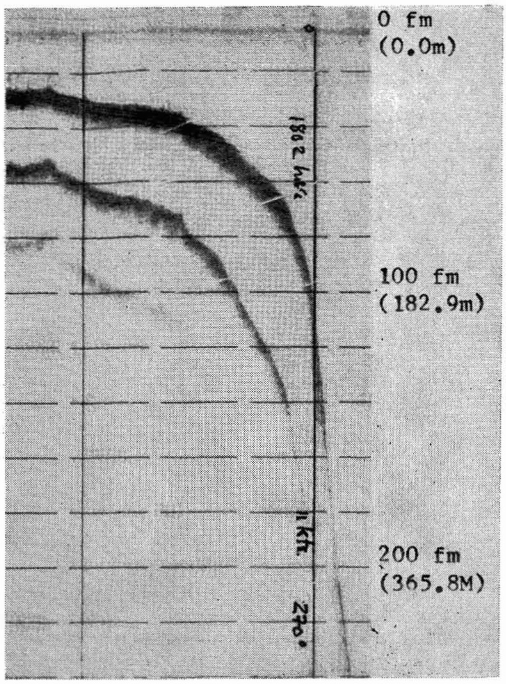

FIG. 1. Profile of the southern flank of Kure. Ship's course was 270° at 11 knots. Depth intervals are 20 fathoms (36.58 m); time lines are 5 minutes. The uppermost trace is the actual profile, the second and third are multiples of the first.

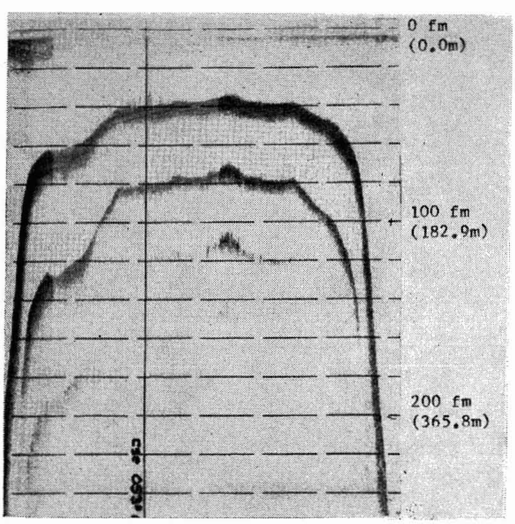

FIG. 2. Profile of Nero Bank. Ship's course was 053° at 11 knots. Depth intervals are 20 fathoms (36.58 m); time lines are 5 minutes. The uppermost trace is the actual profile; the second and third are multiples of the first.

zone a windward and leeward aspect. Each zone has a characteristic coral assemblage (Figs. 3, 4, 5). Observations were all made while skin diving; SCUBA was not available. The distributions and relative abundances of the coral species as well as the reef zone descriptions are a composite summary of numerous nonquantitative surveys. Corals were identified in the field by sight. The identification of a reference collection made by the author from Midway prior to the present field study was checked by Dr. John Wells. During the course of the work, a reference collection was made from Kure. (This collection is presently at Scripps Institution of Oceanography but will be deposited in the United States National Museum).

SEAWARD REEF: The seaward reef extends shoreward from the break in slope at somewhat less than 80 m as a broad terrace to the reef face. The slope is gradual (< 8°). On the windward side relief increases until near the reef face the terrace consists of massive buttresses separated by deep, steep-walled channels oriented perpendicular to the trend of the reef face. Immediately before the reef face the bottoms of the channels are 8 to 9 m below the sea surface or at approximately wave base. They deepen gradually to seaward. The tops and sides of the buttresses, away from the immediate face of the reef, are dotted with colonies of *Pocillopora meandrina noblis* and occasionally *Porites lobata*. The principal

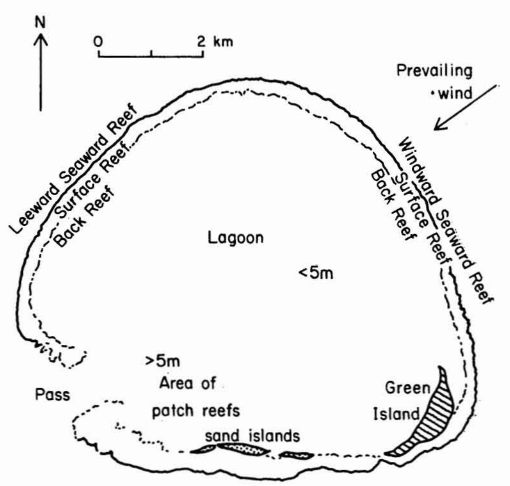

FIG. 3. Plan view of Kure Atoll giving locations of the reef zones. The outline of the atoll was sketched from an aerial photograph (Gross et al., 1969).

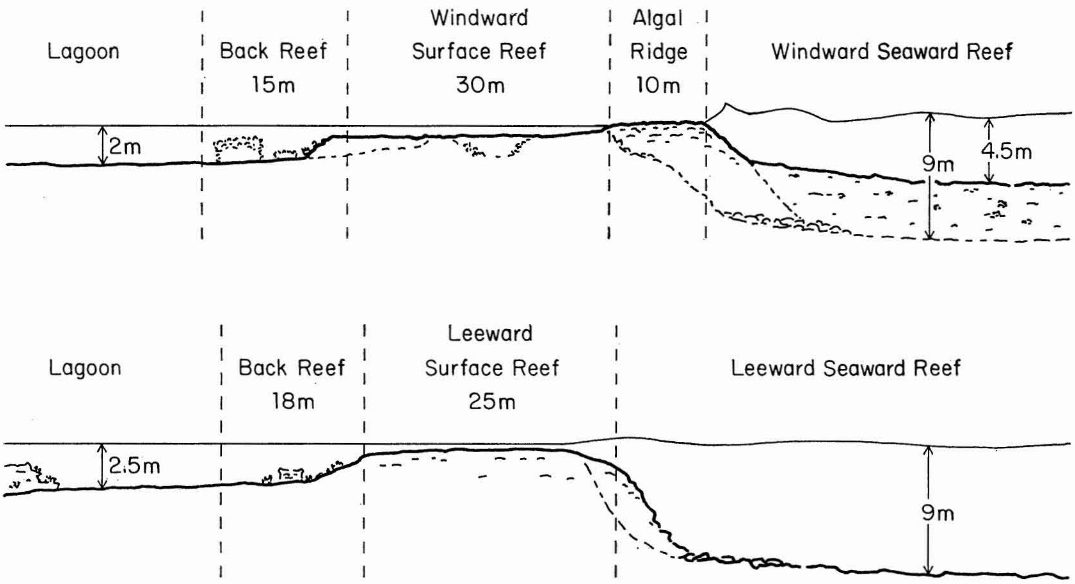

FIG. 4. Cross-sectional view of the various reef zones. These profiles have been generalized from numerous nonquantitative surveys.

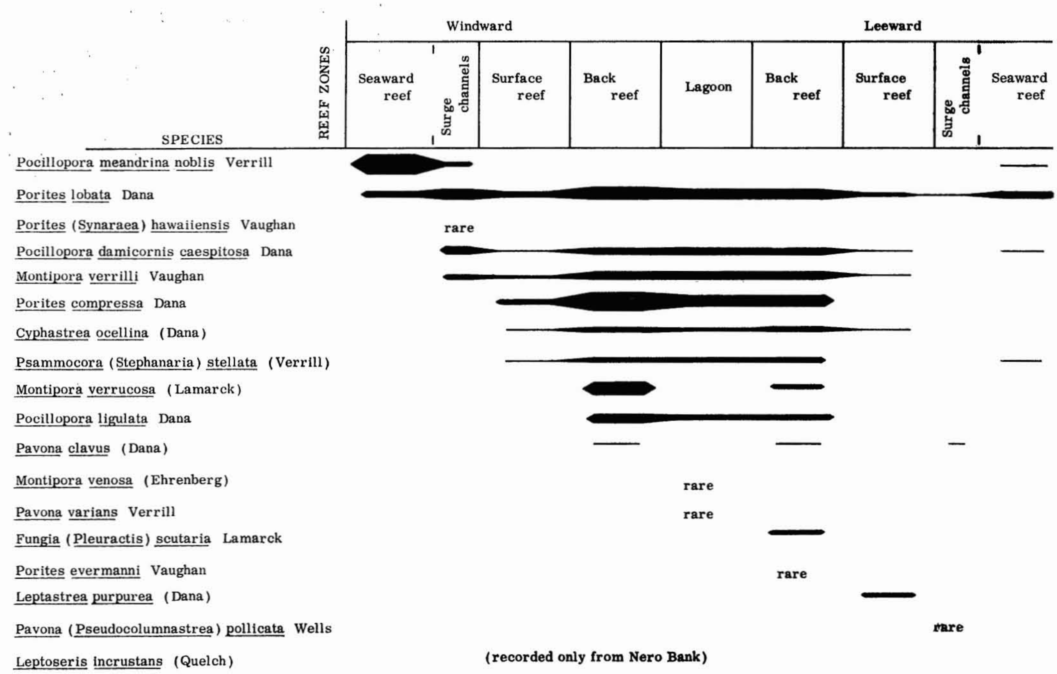

FIG. 5. Relative abundance of each species of hermatypic scleractinian found in each of Kure's reef zones. Abundances are estimates from nonquantitative surveys.

lime-secreting organisms are, however, coralline algae.

The immediate face of the windward reef is highly cavernous, cut by surge channels, and devoid of living coral. The bottoms of the larger and deeper surge channels are cobble filled. Sand fills the bottoms of the channels at depths greater than about 9 m as one progresses away from the face of the reef. At the heads of the surge channels living coral, principally *Porites lobata,* is again encountered.

Proceeding leeward around the atoll, the system of buttresses and channels becomes less coherent and finally disappears almost completely on the western side of the atoll (Fig. 4). Living coral becomes more scarce and the species composition also changes. *Pocillopora meandrina noblis* loses its position of obvious relative dominance and *Porites lobata* becomes relatively more abundant. The extreme leeward seaward reef has virtually no living coral.

SURFACE REEF: The surface reef is nearly circular surrounding a lagoon some 9 km in diameter. Width of the reef is greatest on the windward side, becoming progressively narrower to leeward with the exception of the portion of the southern sector near the sand islands (Fig. 3). A gap or pass of approximately 1.5 km is present in the southwestern sector. Along the inner part of the northern and northeastern sectors a number of sections of consolidated reef debris stand exposed even during normal high tides. An algal ridge occurs only on the windward side of the atoll and there are no living corals growing on it. The surface reef behind the algal ridge, where the ridge is present, and from the reef's seaward edge where the ridge is not present, is a hard and consolidated reef flat covered by a few centimeters of water during normal low tides. The maximum tidal range at Kure is about 0.64 m.

Numerous small shallow channels and pools are present on the windward surface reef, and it is in these that living corals are generally found. *Porites lobata* is the dominant species. However, channels and pools are generally lacking on the leeward surface reef, and, although nearly all the same species are present, coral growth is concomitantly less profuse.

BACK REEF: The immediate lagoonward face of the surface reef, and the lagoon area immediately adjacent to it (usually some 30 m or less in breadth), comprises the back reef zone. Water depth is usually less than 3 m. An irregular series of ledges and terraces descend from the surface reef to a shallow sand bottom occupied by large heads, mounds, and patches of coral. Important species here are *Montipora verrucosa,* especially abundant in the northeastern sector, and *Porites compressa,* which forms large flat-topped heads up to 2 m in diameter. This zone is the richest, both in terms of the number of species present and the relative amount of area covered by living coral.

LAGOON REEFS: The lagoon is nearly 80 percent sediment-filled to depths less than 5 m (Gross et al., 1969). Deeper water is found in the southwestern corner, lagoonward of the pass. Maximum depth is about 15 m. Patch reefs occur chiefly in the southwestern sector in water depths from 2 to 6 m. The amount of living coral present on these patch reefs is highly variable, but algae and algal-covered dead coral generally predominate. *Pocillopora ligulata* and *Porites lobata* are frequently encountered lagoon species (Fig. 5).

Deep Reefs

Information on the occurrence of living coral at depths greater than 15 m is scanty. Two dredge hauls were taken on the south side of Kure: the first in 15 to 35 m of water, the second in 40 to 60 m. Both hauls brought up abundant soft and coralline algae, a variety of invertebrates, several fish, and calcareous debris. The only living corals obtained were two small colonies of *Pocillopora damicornis caespitosa,* which were found in the shallower haul. Another dredge haul in 77 to 115 m of water on nearby Nero Bank (27°59′N, 177°56′W) brought up actively growing coralline algae in the form of spherical concretions and various invertebrates, including a single species of hermatypic coral, *Leptoseris incrustans.*

With the exception of a single species, reef-building corals at Kure appear to be generally restricted to quite shallow water, and no vertical zonation is readily apparent.

ECOLOGICAL FACTORS

Circulation

Scour, mechanical stress, siltation, turbidity, and food supply are all ecological agents affected by the vigor of circulation. Gradients influencing rates of diffusive exchange are also affected by water movements. Heavy surf, particularly during winter storms, exerts great mechanical stress on the seaward reefs and over the surface reefs, especially on the northern and eastern portions of the atoll. Surf also subjects portions of these reefs to severe scour from sand and cobbles. The shallow, largely sediment-filled lagoon becomes increasingly turbid under moderate wind stress and siltation becomes an important factor. The presence of large ripple marks across the shallow lagoon terrace (Gross et al., 1969) is convincing evidence that the shifting distribution of sand is in good part responsible for the paucity of patch reefs in that area. The predominantly northeast to southwest flow of water across the atoll, fluctuating in intensity with the tidal cycle (spring tidal range on Midway according to Gross et al., 1969, is 0.64 m) and wind conditions, creates an upstream-downstream effect in the transport of zooplankton and dissolved organics and gases. Presumably the species composition of the various reef zones reflects these gradients.

Temperature

A survey of bathythermograph records kept at Scripps Institution indicates that a weak thermocline generally develops in the vicinity of Kure by late summer. The depth and strength of the thermocline appears to be quite variable. When best developed, the thermocline begins at a depth of approximately 34 m, where the temperature is near 28°C, and ends at approximately 80 m, where the temperature is near 20°C (Fig. 6). Depths are normally somewhat shallower and temperatures slightly lower. Winter cooling and mixing result in a nearly uniform temperature structure from the surface to about 80 m.

Monthly mean sea surface temperatures measured on Midway (1943–1963) range from 26.9°C in August to 19.2°C in February, with annual mean of 23.1° C (Gross et al., 1969). Optimal temperature range for vigorous coral growth is between 25°C and 29°C (Vaughan and Wells, 1943)—a criterion met at least in shallow water at Kure for 5 months of the year. The mean for the coldest month of the year must not be below 18.5°C for vigorous growth of hermatypic corals to endure (Vaughan and Wells, 1943). This condition is met at Kure to depths approaching 80 m.

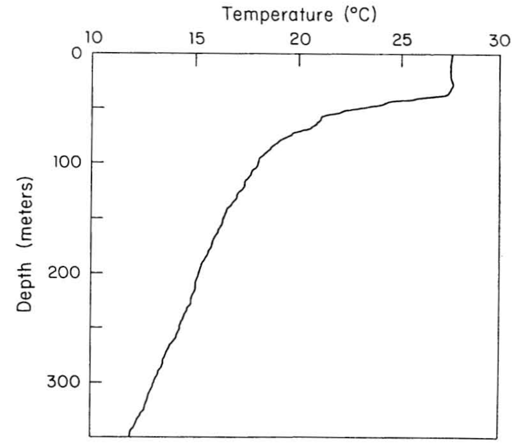

FIG. 6. XBT trace obtained near Kure in early September 1968, showing unusually well-developed thermocline.

All of the hermatypic genera and subgenera found in the more southerly and warmer Hawaiian Islands that are not either extremely rare or of unsubstantiated occurrence (a total of 12) except one, *Madracis,* are also found at Kure. However, the number of species appears to be only about one-half. (Dr. J. W. Wells, personal communication, lists five possible additional species collected by the U.S. Geological Survey from Midway and Kure for which I have no ecological data, bringing the species total there to 23.) The reduction in the number of species may be related to temperature, but also may simply reflect a reduction in island area (MacArthur and Wilson, 1967). By comparison, 33 species in 21 genera and subgenera, including *Acropora,* are listed as occurring in Tateyama-wan (35°10′N) and Enoura-wan (35°05′N), the northernmost localities of reef corals in Japan (Yabe and Sugiyama, 1935). Mean monthly seawater temperatures in those localities fall below 13° C for the coldest month of the year, and coral growth extends to a depth of at least 40 m. However, when all three subfaunas of Japan are combined, more than 200 species in 40-plus genera and subgenera are found (Yabe and Sugiyama, 1935). Further, six widespread Indo-Pacific genera, including two not found at Kure (or any of the Hawaiian Islands), occur well beyond the southern extremity of the Great Barrier Reef, where temperature falls to between 12° to 13° C (Wells, 1955). Therefore temperature, while undoubtedly a critical factor limiting the distribution of all hermatypic species, does not presently appear to be the major factor limiting the total species complement nor the depth distribution of corals at Kure.

Time

Dr. J. W. Wells, who is examining the corals obtained in the Midway drillings, states that the present fauna is somewhat attenuated in comparison to that of the Miocene (Ladd et al., 1967). Three hermatypic genera absent from present-day Hawaiian reefs were present in the past (Menard, Allison, and Durham, 1962; Durham, 1964). The occurrence of a fourth, *Acropora,* the coral genus containing the greatest number of species (Wells, 1956), and a conspicuous dominant over large areas of reef throughout the Indo-West-Pacific, is extremely limited today. Dr. Edwin C. Allison (personal communication) now believes these fossil materials reported by Durham to be late Pliocene or early Pleistocene in age. Depauperization of the coral fauna at Kure during the Pleistocene may have been even greater than for the southern major islands. As the southern major Hawaiian Islands are undoubtedly the principal source region for immigrant species traveling up the chain of island stepping stones to Kure, the relative depauperization of the Hawaiian coral fauna is germane to considerations of why there are so few species present at Kure. Occupying an isolated zoogeographical position as they do, the question then is whether conditions in the Hawaiian Islands today are simply unfavorable for many coral species, or whether many species have not as yet been successful in invading or recolonizing these islands, or whether both these factors are operating together.

Larval Transport

As suggested by Vaughan as early as 1907, the factor most likely limiting the present number of coral species found in the Hawaiian Islands is lack of successful larval transport, and, indeed, the attenuation of coral genera from west to east in the Pacific noted by Wells (1954) without a noticeable change in local environmental factors substantiates this contention. No doubt the relative richness of the Japanese fauna is the result of larval influx with the strong Kuroshio Current.

Species-specific laboratory studies on the free-floating period of coral larvae done in Palau by Abe (1937) and Atoda (1947 *a, b;* 1951 *a, b, c*), on the Great Barrier Reef by Stephenson (1931), and in Hawaii by Edmondson (1929) indicate no trend that would lead to generalizations regarding distribution; i.e., those species having the longest laboratory free-floating existence are not necessarily the most widely distributed. The only species studied which is common to both the Hawaiian area and Palau is *Pocillopora damicornis caespitosa.* In Palau, where the temperature was between 26° C and 30° C, all planulae of this species settled within 9 days, with greater than 50 percent in the first 2 days (Atoda, 1947 *a*). In Hawaii, where the temperature was between 24° C and 27° C, settlement took from 3 to 18 days (Edmondson, 1929). As a result of his experiments Edmondson stated that warmer temperatures hasten settlement and attachment. Consequently, larvae transported into, or originating in, cooler waters might be expected to have slightly longer free-floating periods resulting in transport over greater distances. However, as Kawaguti (1944) pointed out, thigmotaxis, phototaxis, geotaxis, and rheotaxis are all involved in the settlement and affixation of coral planulae. Behavior during, as well as the length of, the free-floating period may be an equally important factor governing the distribution of coral species.

The similarity of coral faunas from Hawaii in the northern hemisphere (Vaughan, 1907) and the Marquesas in the southern hemisphere (Crossland, 1927) eastward to the western continental margin of the Americas (Durham, 1966) suggests that only a limited number of coral genera contain species which are capable of crossing broad oceanic barriers.

SUMMARY

1. A long and complex history has led to the establishment and maintenance of an atoll at 28°25′ north latitude—outside the tropics.

2. The atoll can be divided into four major reef zones, each with a characteristic coral assemblage.

3. The vigor of circulation resulting from wave action and tidal fluctuations is probably the principal macroscopic parameter governing the distribution of corals in shallow water at Kure.

4. Although Kure's temperature regime is undoubtedly suboptimal for many, if not for most, species of hermatypic scleractinians, comparative temperature data suggest that more should be able to survive there than are currently present.

5. A relative inability of the larvae of many coral species to cross deep oceanic barriers, resulting in long time constants for invasion or recolonization of distant areas, may be the major factor presently limiting the number of living species at Kure.

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